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EVOLUTION OF JAW DISPARITY IN FISHES

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Abstract: The morphology of the vertebrate lower jaw has been used to infer feeding ecology, with transformations in mandibular shape and structure likely to have facilitated the emergence of different feeding behaviours in vertebrate evolution. Here we present elliptical Fourier shape and principal component analyses, characterizing and comparing the disparity of jaw shape in early gnathostomes and their modern primitively aquatic counterparts. 83% of shape variation is summarized on the first three principal component axes and all component clades of early gnathostomes exhibit overlapping morphological variation. Non-tetrapodomorph Palaeozoic sarcopterygians are more disparate than their extant counterparts whereas extant chondrichthyans are more disparate than their Palaeozoic counterparts. More generally, extant jawed fishes are more disparate than their Palaeozoic

relatives largely because of the extensive shape variation exhibited by mandibles of extant actinopterygians. Only some areas of shape space vacated by Palaeozoic gnathostomes have been convergently refilled by living taxa. Characterization of theoretical jaw morphologies demonstrates that fewer than half of all possible shapes are realized by the jawed fishes that comprise our empirical dataset; many of these morphologies are realized by unrepresented terrestrial tetrapods, implying environmental constraint. Our results are incompatible with the early burst model of clade evolution and contradict the hypothesis that maximum disparity is reached early in the evolutionary history of jawed fishes.

Key words: disparity, lower jaw, shape analysis, morphospace, gnathostomes, macroevolution.

THE lower jaw has been considered to be a key innovation that underpinned the evolutionary radiation of gnathostomes, leading ultimately to the displacement of their jawless relatives. While the diversification of early jawed vertebrates and the disparity of feeding behaviours have been considered previously (Hulsey & Wainwright 2002; Anderson 2008; Anderson *et al.* 2011) jaw shape itself has been little studied (Neenan *et al.* 2014), which is perhaps surprising since jaw shape should be correlated strongly to function. Anderson *et al.* (2011) demonstrated that disparity of functional characters associated with gnathostome feeding plateaued soon after the origin of the jaw, but they did not consider the evolution of gnathostomes beyond their initial radiation or the implications of mandibular innovation. Anderson *et al.* (2013) explored this topic in stem-tetrapods; here we quantify jaw shape in modern and Palaeozoic jawed fishes and explore shape disparity during the initial gnathostome radiation, bench-marked against the disparity of modern jawed fishes. We restrict our analysis to the paraphyletic grade of jawed fishes to allow us to explore the radiation of jawed vertebrates while excluding the impact of adaptation to the terrestrial environment. We test whether the full extent of jaw morphological variation was established

early in gnathostome evolutionary history, consistent with an early burst model of morphological evolution (Simpson 1944; Givnish 2015), or whether extant jaw morphological diversity exceeds that of Palaeozoic fossil taxa. Here, early burst refers to a pattern of high early disparity (e.g. Simpson 1944) not a comparative phylogenetic model of exponentially decreasing rates of evolution through time (e.g. Harmon *et al.* 2010). Finally, through characterization of theoretical jaw shapes throughout morphospace, we explore the reasons for variance in morphospace occupation and potential functional constraints.

MATERIAL AND METHOD

Taxon sampling

We sampled 138 gnathostome species from all principal grades of early jawed vertebrates, *viz.* placoderms, acanthodians, chondrichthyans, actinopterygians and non-tetrapodomorph sarcopterygian fish. Taxa were chosen to represent taxonomic orders and families from two intervals: the initial radiation of gnathostomes in the Siluro-Devonian (443.8–358.9 Ma) vs the Recent. We excluded

mandibles where the outline could not be defined because of incomplete preservation. Data, supplementary figures, tables, and methods descriptions are available in Hill *et al.* (2018). Hill *et al.* (2018, table S1) provides a complete list of specimens used. The sample size is taxonomically and phylogenetically broad enough that large-scale differences in morphology should be recognized.

Morphometric and disparity analyses

Our study focuses on the quantification of geometric shape variation in the lateral jaw profile. Inevitably, this subsamples available information on jaw geometry. However, previous studies have shown that two dimensional data affords an effective approximation of three dimensional data when the parameters that define shape occur primarily in two dimensional space, as in the hemimandibles studied here (Álvarez & Perez 2012; Cardini 2014; Buser *et al.* 2018). Digitized jaw outline data were recorded and dentition was excluded to isolate the jaw shape (Hill *et al.* 2018, figs S1, S2). Images were imported into R (R Core Team 2016) in which the packages Momocs (Bonhomme *et al.* 2014) and Vegan (Oksanen *et al.* 2013) were used to quantify variation in lower jaw morphology. A Procrustes transformation was performed to remove the effects of size, position and rotation. The outlines were defined by 200 coordinates starting at the rostral tip of the jaw. Outlines were further analysed using elliptical Fourier transformation, decomposing outlines into a series of closed curves or harmonics. The use of too many harmonics exposes the outlines to high-frequency noise and using too few risks loss of morphological detail; following Crampton (1995), we used 10 harmonics to gauge 99% of the total shape variation. A principal component analysis (PCA) was applied to the Fourier coefficients and the resulting principal component (PC) scores were used to plot empirical morphospaces. To assess the statistical significance of variation in shape between clades and between their living and fossil representatives, we calculated pairwise-comparisons using non-parametric multivariate analyses of variance (NPMANOVA) for all clades in both the initial radiation and extant datasets using the *Adonis* function in Vegan (Oksanen *et al.* 2013). Disparity for subgroups is also summarized using the sum of variances metric, measured from all 40-PC axes accounting for total variation, in R (R Core Team 2016); the partial disparity metric was calculated from the first 7-PC axes using MDA (Navarro 2003). We characterized morphological variation across each of the first seven component axes; the mean shape is a simple rod or beam shape at the origin of the morphospace and subsequent forms are defined (or not) by their standard deviation from the mean shape. The jaw shapes are created by

using the *PC.contrib* function in Momocs (Bonhomme *et al.* 2014) which calculates and plots shape variation along the PC axes. Density plots or heat maps were also generated by using the *kde2d* function in MASS v 7.3-47 (Ripley & Venables 2002) to show the distribution density of both fossil and extant specimens.

RESULTS

Most lower jaw shape variation is accounted for by a relatively small number of axes. 95% of variation is accounted for within the first seven PC-axes, and 83% of the variation is summarized on the first three axes (Hill *et al.* 2018, figs S3, S4). The main morphological trend on PC1 (52.3% variation) is associated with curvature of the proximal–distal axis of the mandible, while PC2 (21% of shape variation) is associated with variation from long and slender to comparatively short and deep mandible morphologies. Variation on PC3 (11%) represents a trend where the back of the lower jaw is either angled and curved dorsally, making the mandible appear convex or angled ventrally at the anterior tip of the jaw, making the mandible appear more concave overall (Figs 1, 2).

Partial disparity estimates (Hill *et al.* 2018, table S2) show the relative contribution of extant and Palaeozoic taxa of major gnathostome groups to overall disparity. Actinopterygians contribute more than half of the morphological disparity (60%), followed by chondrichthyans (18%), placoderms (12%), non-tetrapodomorph sarcopterygian fish (5%), and acanthodians (5%). The component groups exhibit overlap on PCs 1, 2 and 3 (Fig. 1), and most taxa are clustered about the centroid (Figs 1, 3). However, when all seven PC-axes are considered, all groups occupy statistically distinct regions of morphospace (at $p \leq 0.05$; Hill *et al.* 2018, table S5), except for acanthodians and sarcopterygians which are indistinct from actinopterygians. The extremes in morphospace occupation are defined by actinopterygians, chondrichthyans and the placoderm *Brontichthys* (Fig. 1).

The initial radiation dataset is comprised of 75 Silurian and Devonian taxa. Almost all component clades of early gnathostomes significantly exhibit overlapping disparity (Fig. 4), the exception being fossil actinopterygians, which account for only 9% of the total fossil lower jaw shape variation. However, like fossil chondrichthyans, fossil actinopterygians have lower jaws that are deeper and more robust in shape than the other fossil clades. Placoderms overlap most with other clades (fossil partial disparity 36%; Hill *et al.* 2018, table S3), even though the shape of the anterior and posterior regions of the lower jaw of placoderms is intrinsically distinct from that in other fossil clades. Both chondrichthyans and acanthodians each account for 18% of the overall fossil jaw shape

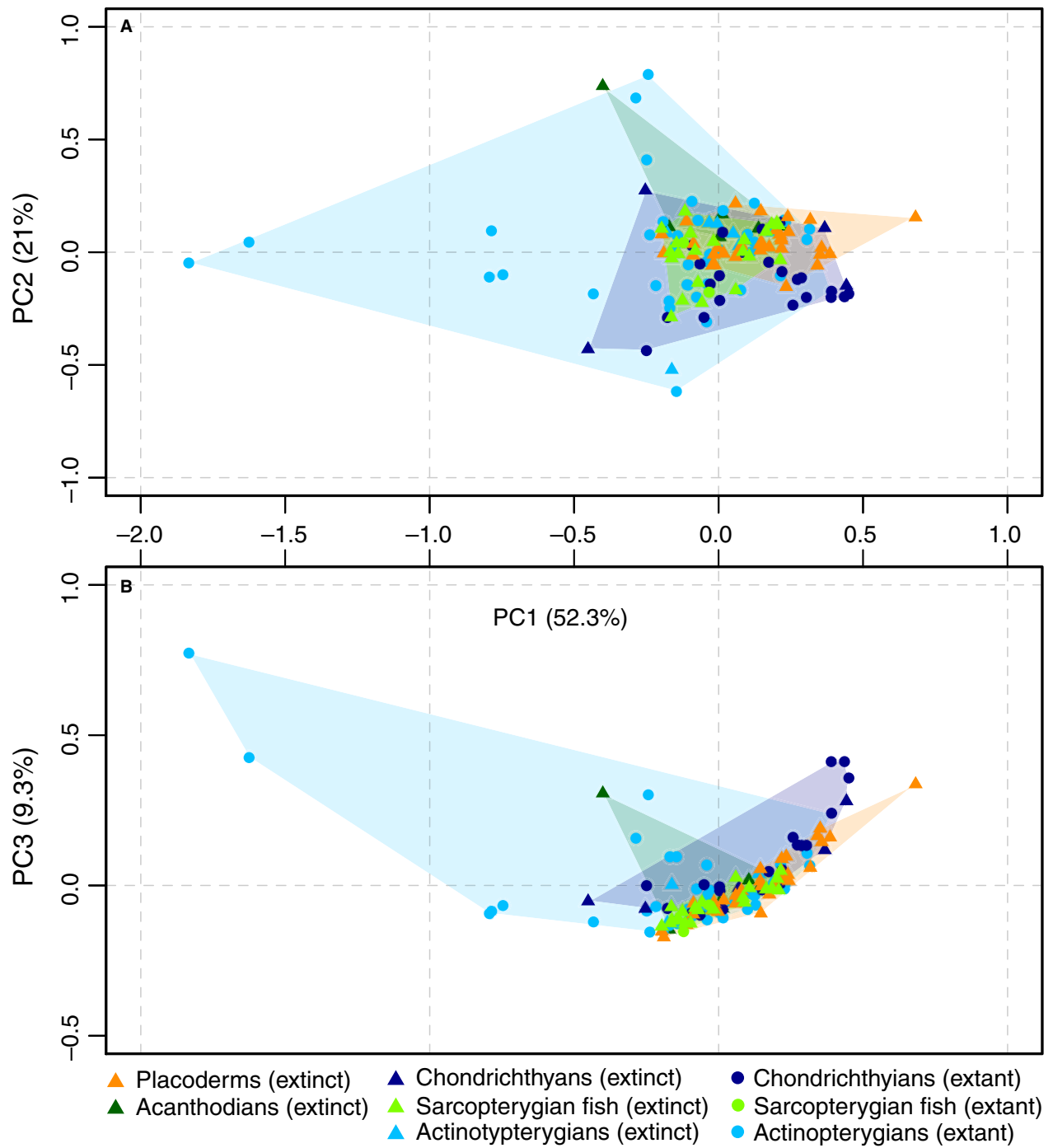


FIG. 1. Disparity of jaw morphologies in living and fossil jawed fishes. A, principal component axis (PC)1 vs PC2. B, PC1 vs PC3. Colour online.

variation, whereas fossil sarcopterygians account for 19% of the total shape variation (Hill *et al.* 2018, table S3) and are more disparate in the Palaeozoic than among their extant counterparts (extant partial disparity 1%; Hill *et al.* 2018, table S4).

In the extant morphospace, actinopterygians spread far from the centroid (Fig. 4C) and occupy a statistically

different morphospace region compared to all other clades of extant taxa. Living chondrichthyans are also statistically distinct from other extant clades (partial disparity 20%; p -value = 0.001); the vertical height (depth) of the mandible decreases, and the posterior portion of Meckel's cartilage morphs into a bulbous shape like the condylar processes of other gnathostomes. Extant

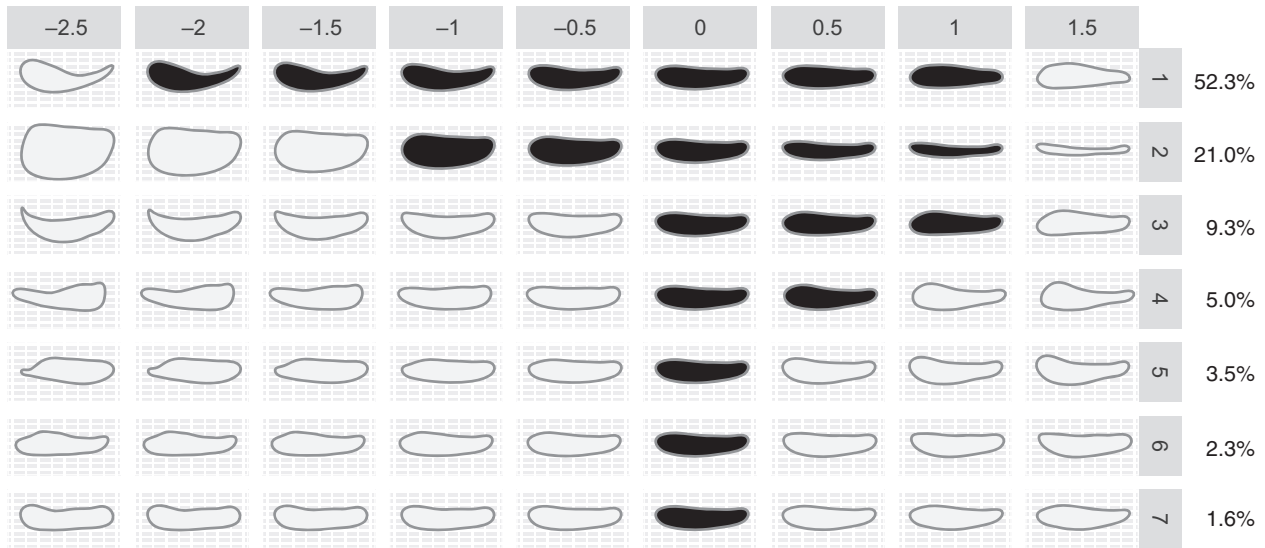


FIG. 2. Variance in jaw morphologies for each of the principal component axes. Realized morphologies (shaded) constitute fewer than half of theoretical jaw shapes based on our dataset of jawed fishes. Percentage values represent variance per PC axis.

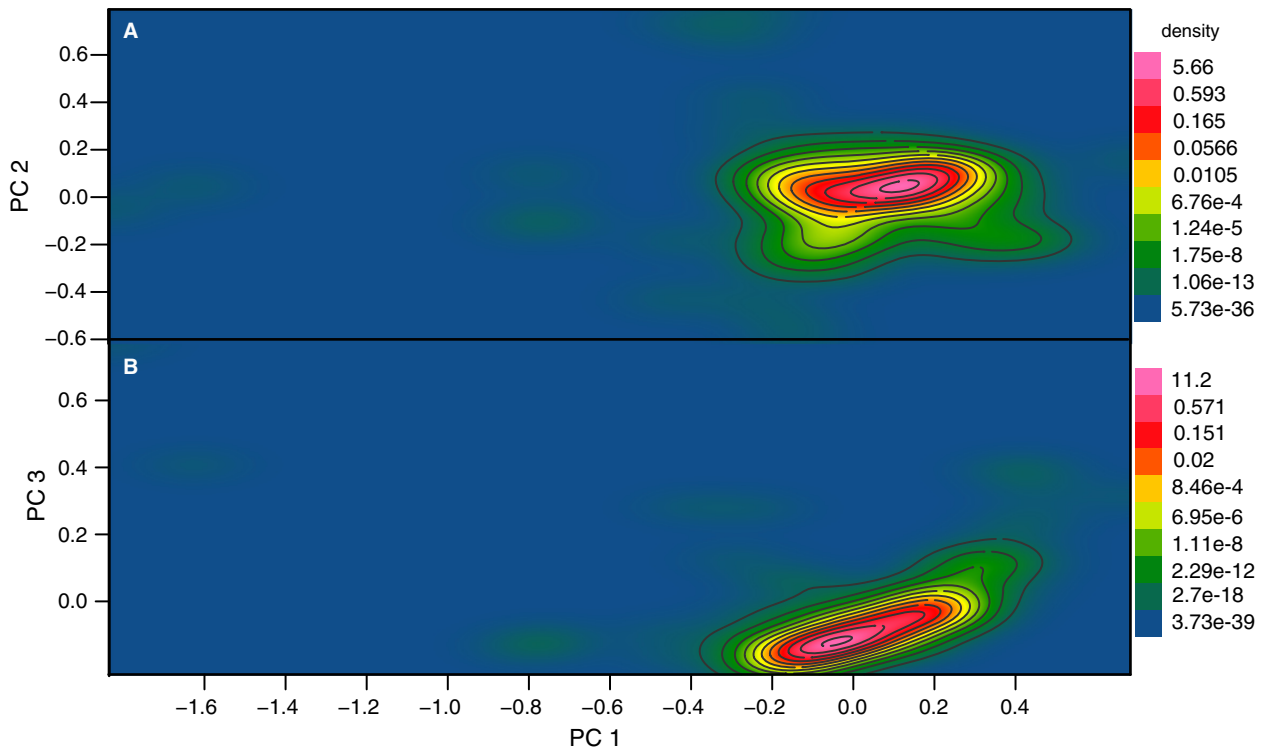


FIG. 3. The density of morphospace occupation for all fossil and living jawed vertebrates in our dataset. A, principal component axes (PC)1 vs PC2. B, PC1 vs PC3. Colour online.

actinopterygians and chondrichthyans are more disparate than their Palaeozoic counterparts (Hill *et al.* 2018, table S2). Extant sarcopterygians are only a small relict of early modern aquatic jawed vertebrates (partial

disparity 1%; p -value = 0.644; Hill *et al.* 2018, fig. S4). Extreme morphologies for extant taxa are defined by actinopterygians, chondrichthyans and sarcopterygians (Fig. 4C, D).

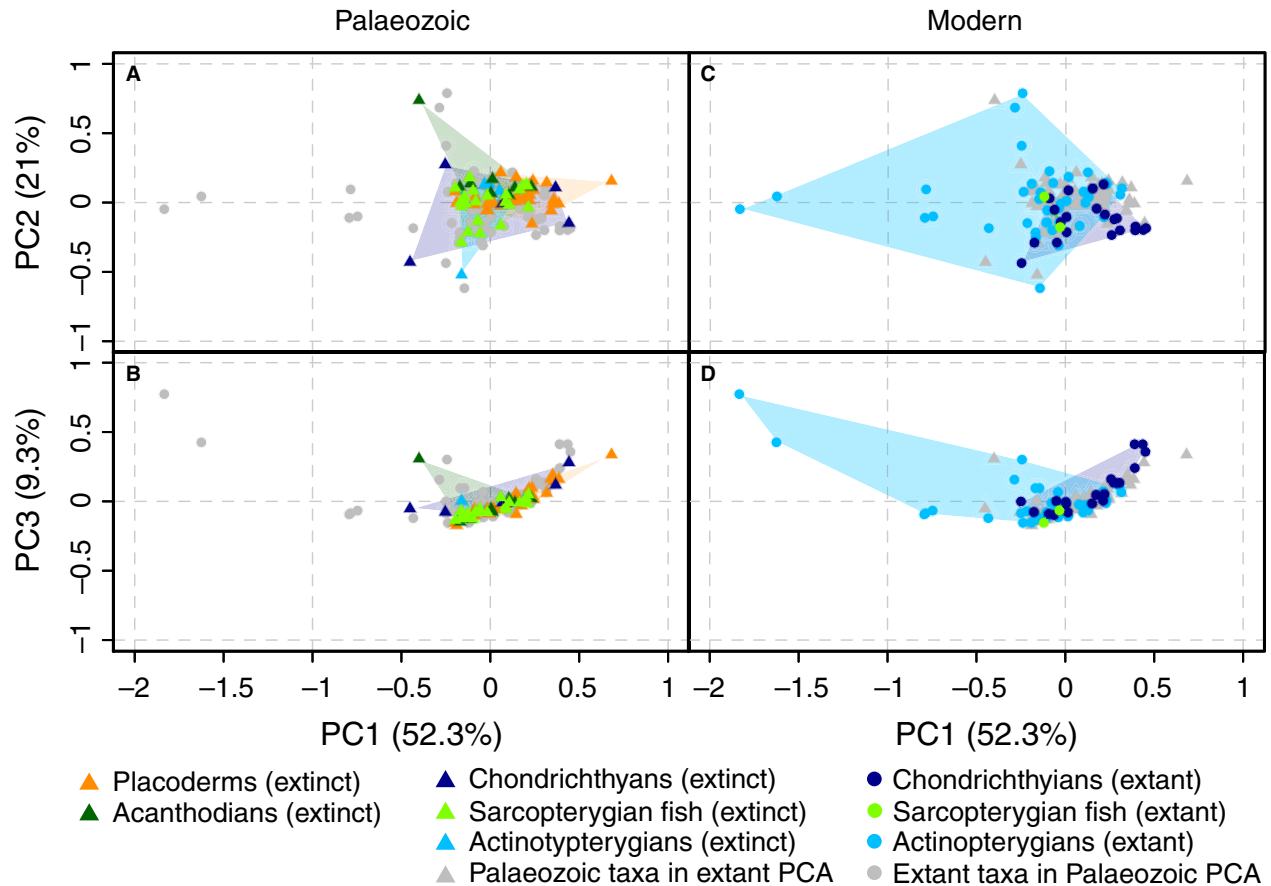


FIG. 4. Disparity of jaw morphologies in living vs fossil jawed fishes. A–B, Palaeozoic (Silurian–Devonian) jawed fishes: A, principal component axis (PC)1 vs PC2; B, PC1 vs PC3. C–D, living jawed fishes: C, PC1 vs PC2; D, PC1 vs PC3. Colour online.

DISCUSSION

Our characterization of the variation in lower jaw morphology across the PC axes (Fig. 2) indicates that most of the variation on the first axis (52.3% variance) concerns the curvature of the proximal–distal axis of the mandible, and on the second axis (21% variance), from long slender mandibles to comparatively short and deep morphologies. These patterns suggest a strong functional control on mandibular morphologies, with the axes varying between morphologies with lower vs higher mechanical advantage (faster vs more forceful closure of the jaw due to shifts in adductor leverage) and robusticity, respectively (Anderson *et al.* 2011). This is because more curved jaws may increase the length of the in-lever of muscle action and shorter jaws may decrease the out-lever to the bite point; both are advantageous in increasing the leverage of the jaw. A convex jaw shape present on negative axis 3 corresponds with the jaw hinge dropped ventral to the tooth row margin, a characteristic associated with herbivory or crushing feeding and vice-like adduction of the tooth row (Turnbull 1970; Ramsay & Wilga 2007). Axis 4

demonstrates a shift in jaw morphology from a deep symphysis to a deep articular region of the jaw. A deep proximal articular region provides increased surface area for adductor muscle attachment; in amniotes, deep symphyseal regions are associated with fusion or secure association of mandibular rami to assist with resistance to large bite forces or shaking and twisting loads (Holliday & Nesbitt 2013; Wainwright & Longo 2017).

Actinopterygians exhibit the greatest amount of variance on the first three principal component (PC) axes (Fig. 1A, B). Setting these aside, the variance in mandibular morphology exhibited by Palaeozoic and Recent jawed fishes is very similar (Fig. 4). Most clades exhibit considerable overlap in morphospace occupation, with only the placoderm *Brontichthys*, acanthodians and chondrichthyans departing significantly from the most densely occupied regions of morphospace shared by all Palaeozoic clades (Fig. 4A, C). This provides some corroboration of the hypothesis of an initial increase followed by stabilization in the disparity of functionally important mandibular characters (Anderson *et al.* 2011) and morphological traits generally. However, despite the general similarity in

morphospace occupation exhibited by living and Palaeozoic non-actinopterygian fishes, some groups exhibit evidence of displacement, with the chondrichthyans shrinking in disparity relative to the variance of their Palaeozoic chondrichthyan and acanthodian counterparts (Fig. 4A, C vs B, D). Sarcopterygian fishes are dramatically diminished and the distinct regions of morphospace occupied by some Palaeozoic placoderms remain unoccupied in the morphospace of extant fishes.

The general stability in mandibular morphology warrants discussion of its material basis. Each of the component clades and grades may have converged on a generalized morphology (or failed to diverge from it) because it represents a functional optimum, although the dramatic expansion in disparity exhibited by extant actinopterygians relative to their Palaeozoic counterparts speaks against this. Differences in the composition of the mandible in many of the Palaeozoic groups, at least as characterized, suggest that stabilization in jaw morphology is not a consequence of fabricational constraint. We characterized the mandibular morphology of placoderms in terms of their dermal infragnathal, which is topologically and compositionally distinct from the cartilaginous (and usually unfossilized) Meckel's cartilage. Conversely, the mandible of chondrichthyans is essentially cartilaginous, while in osteichthyans, the mandible encompasses both the dermal fascia and a largely enclosed Meckel's cartilage. This suggests that the Palaeozoic stabilization in the variance of mandibular functional characters (Anderson *et al.* 2011) and of morphology, is functional, perhaps an adaptive optimum given the attendant feeding ecologies exhibited by early jawed vertebrates (see e.g. Janvier 1996).

Nevertheless, the most obvious difference in morphospace occupation between the Palaeozoic and Recent censuses, is the dramatic expansion in the range of variation exhibited by actinopterygians and, among them, teleosts. This is achieved not only through the occupation of previously unoccupied regions of morphospace, but through expansion to encompass much (but not all) of the morphospace occupied by placoderms, acanthodians, chondrichthyans, sarcopterygians, as well as Palaeozoic actinopterygians. Most of the newly occupied regions of morphospace are captured as variance on PC 1, characterized by increased curvature of the mandible (Fig. 2). It is notable that those actinopterygians that expand the envelope of gnathostome mandible morphospace beyond that achieved by other clades (*viz.* *Lophius*, *Halosauropsis*, *Ariopsis*, *Malapterurus*, *Cnidio-glanis*, *Gadus*, *Arothron*) are all teleosts, the majority of which are acanthomorphs. The evolution of jaw protrusion may, therefore, underlie this foray into hitherto unoccupied morphospace, as might the evolution of pharyngognath (e.g. the elopomorph outlier

Gymnothorax) which facilitates the functional partitioning of the mandibular and pharyngeal jaw systems (Wainwright & Longo 2017), perhaps facilitating the innovation of new mandibular morphologies.

Despite the dramatic increase in variance and morphospace occupation brought about by actinopterygian and teleost diversification, most of morphospace circumscribed by our analyses remains unoccupied, rather than occupied (Figs 1–4). This is particularly clear in our characterization of mandibular morphological variation across the first seven PC axes (Fig. 2) in which only about half of the representative morphologies are realized by any of the Palaeozoic or Recent vertebrates included in our analysis. Morphospace occupation is often rationalized in terms of functional and developmental constraints on realizing all possible morphologies, and time required for their exploration (Seilacher 1970). In terms of the sum of lineages represented, our census of morphospace occupation constitutes substantially greater than the 400 million years that have elapsed since the evolutionary emergence of jawed vertebrates and so time might not be a significant explanatory factor. Though some are certainly peculiar, the majority of the 'unrealized' mandibular morphologies in Figure 2 are not so unusual that they might be suspected to be developmentally or functionally impossible. Indeed, many of the 'unrealized' morphologies strongly resemble the mandibles of terrestrial vertebrates, which we have not considered in our analysis. This warrants a comparative analysis of tetrapods and a greater sampling of extant fishes, but it also suggests that the mandibular morphologies unsampled in our analysis are absent because of environmental constraints and the differences in feeding ecology exhibited by tetrapods in comparison to fishes.

While the results of our analysis corroborate the previous observation of an initial burst of variance in the disparity of functional mandibular characteristics followed by stabilization (Anderson *et al.* 2011), our longer temporal perspective shows that mandibular morphologies have undergone a substantial increase in variance, but the bulk diversity remains in a mean area of morphospace. This pattern of episodically increasing variance is incompatible with a general 'early burst' model of maximal initial disparity for gnathostomes as a whole (Erwin 2007; Hughes *et al.* 2012), but compatible with evidence from extant phylogenetic data (Harmon *et al.* 2010; but see Slater & Pennell 2014; Puttick 2017).

CONCLUSIONS

Gnathostome clades are distinct in jaw shape in both the past and the present. Initially restricted shape variance is followed by a marked increase in morphological disparity

after the emergence of modern actinopterygians, associated with a decrease in shape variance of sarcopterygian fish. Overall this illustrates that living faunas are more disparate than fossil faunas representing early gnathostomes. This contradicts previous studies (Hughes *et al.* 2012) where initial maximum disparity is reached early in evolutionary history. Therefore, our results are incompatible with the early burst model of clade evolution and the hypothesis that maximal jaw disparity is achieved early in gnathostome evolutionary history. Our exploration of early jawed vertebrate morphospace reveals that only some ecological niches have been convergently refilled with modern taxa across time and that unoccupied spaces or gaps within the morphospace are crucial for understanding how lower jaw morphospace occupation is affected through time by historical, functional, temporal, ecological and environmental factors.

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DATA ARCHIVING STATEMENT

Data and supporting material for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cq5ff51>

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1. A lateral profile showing the orientation of the lower jaw as formatted in outline analysis with the posterior portion of the jaw at the left and the most anterior tip at the right.

Figure S2. A colour coordinated panel of lateral lower jaw profiles for all 138 specimens, which corresponds directly with the specimens as listed in Table S1

Figure S3. Percentage of variance on each principal component axis.

Figure S4. Scree plot of the first seven principal components (solid blue line) showing associated eigenvalues plotted against the axis order. The intersection of the broken stick model (dashed red line) with the scree plot indicates that at least 2 axes should be retained for analysis.

Figure S5. The cumulative sum of harmonic power. Harmonic power is proportional to harmonic amplitude and is considered to be a measure of shape information.

Table S6. Pairwise multivariate analysis of variance tests (MANOVA) for the Sil-Dev dataset by clade/group.

Table S7. Pairwise multivariate analysis of variance tests (MANOVA) for the Extant/Living dataset by clade/group.

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